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Interpopulation Genetic Variance after Reciprocal Recurrent Selection in BSSS and BSCB1 Maize Populations

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Abstract

Reciprocal recurrent selection is a breeding procedure designed to improve two populations simultaneously by selecting for performance in the interpopulation cross. The objective of this study was to evaluate the effects of II cycles of selection on the mean, genetic variance, and correlations amongtr aits in the interpopulationc ross of the Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic no. 1 (BSCBI) maize (*Zea mays* L.) populations. Oneh undredr eciprocal full-sib families from Cycle 0, Cycle 5, and Cycle II of the interpopulation cross between BSSS and BSCBI were evaluated at two locations in 1989 and three locations in 1990. Grain yield increased 0.25 Mg ha^{-1} per cycle (6.46%) after II cycles of selection, grain moisture increased 0.85 g kg^{-1} per cycle, root lodging decreased 0.23%, and stalk lodging decreased 1.64% (all changes significant at $P = 0.01$). Estimates of genetic variance for all traits were significantly different from zero, except for root lodging in Cycle II. Genetic variance for grain yield decreased after II cycles of selection, although the differences among cycles were not significant. Root lodging, stalk lodging, anthesis date, and silking date had significant decreases in genetic variance after II cycles of selection. Changeisn heritability generally paralleled changes in genetic variance. Genotypic and phenotypic correlations were seemingly unchangeda cross cycles of selection. The results indicate that reciprocal recurrent selection has been effective in increasing the mean performance of the population cross while maintaining genetic variance.

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Interpopulation Genetic Variance after Reciprocal Recurrent Selection in BSSS and BSCB1 Maize Populations

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ABSTRACT

Reciprocal recurrent selection is a breeding procedure designed to improve two populations simultaneously by selecting for performance in the interpopulation cross. The objective of this study was to evaluate the effects of 11 cycles of selection on the mean, genetic variance, and correlations among traits in the interpopulation cross of the Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic no. 1 (BSCB1) maize (*Zea mays* L.) populations. One hundred reciprocal full-sib families from Cycle 0, Cycle 5, and Cycle 11 of the interpopulation cross between BSSS and BSCB1 were evaluated at two locations in 1989 and three locations in 1990. Grain yield increased 0.25 Mg ha^{-1} per cycle (6.46%) after 11 cycles of selection, grain moisture increased 0.85 g kg^{-1} per cycle, root lodging decreased 0.23%, and stalk lodging decreased 1.64% (all changes significant at $P = 0.01$). Estimates of genetic variance for all traits were significantly different from zero, except for root lodging in Cycle 11. Genetic variance for grain yield decreased after 11 cycles of selection, although the differences among cycles were not significant. Root lodging, stalk lodging, anthesis date, and silking date had significant decreases in genetic variance after 11 cycles of selection. Changes in heritability generally paralleled changes in genetic variance. Genotypic and phenotypic correlations were seemingly unchanged across cycles of selection. The results indicate that reciprocal recurrent selection has been effective in increasing the mean performance of the population cross while maintaining genetic variance.

EVER SINCE native Americans began to transform teosinte [*Zea mays* subsp. *mexicana* (Schrader) Iltis; syn. *Zea mexicana* (Schrader) Kuntze] into domesticated maize, humans have tried to improve the value of maize. The first attempts came via mass selection of phenotypically superior ears or spikelets in open-pollinated populations. These seed-producing structures were bulked and used for the next season's crop, and then selections were made again. This simple breeding method is thought to have transformed teosinte to maize in ≈100 generations (Galinat, 1988).

Mass selection in open-pollinated populations was used for thousands of years as the basis for maize improvement, until Shull (1908, 1909) proposed utilizing hybrids developed from inbred lines. This proposal led to the development of many new selection methods, including recurrent selection based on progeny evaluation.

Recurrent selection can be divided into two categories: intra- and interpopulation methods. Jenkins (1940) and Hull (1945) each proposed intrapopulation recurrent selection methods based on evaluation of half-sib progenies. Jenkins, of the belief that additive genetic effects are most important, suggested selection based on tests of general combining ability by using a broad-based tester in evaluation trials. Hull, in contrast, believed that overdominance is more prevalent, and suggested that breeders should select on the basis of specific combining ability by using a narrow-based tester in evaluations.

Seeing that both methods of selection could be applicable, Comstock et al. (1949) proposed an interpopulation recurrent selection method now known as reciprocal recurrent selection. They proposed starting a recurrent selection program with two broad-based divergent populations. Because the ultimate goal of maize breeders is the development of superior hybrids, parents are selected on the basis of their performance in crosses with the reciprocal population. Combinations of alleles that contributed to the best hybrids would therefore be selected. G.F. Sprague put this theory into practice in 1949 at the Cooperative Federal–State maize breeding program in Iowa. He selected 'Iowa Stiff Stalk Synthetic' (BSSS) and 'Iowa Corn Borer Synthetic no. 1' (BSCB1) to begin the program. This program is currently in the 13th cycle of selection.

The success of a recurrent selection program is determined by evaluating improvement in the mean of the target population, as well as the best individuals within that population. Changes in mean performance occur by increases in the frequency of favorable alleles in the population. The recurrent selection program should also maintain the genetic variability within the population, to facilitate improvement in future cycles of selection. The objective of our study, therefore, was to evaluate the changes in means, frequency distributions, genetic variance, heritabilities, and correlations among traits after 11 cycles of reciprocal recurrent selection in the interpopulation cross of BSSS and BSCB1.

MATERIALS AND METHODS

Genetic materials used for this experiment were derived from BSSS and BSCB1. BSSS was developed in the early 1930s by intercrossing 16 inbred lines chosen for above-average stalk quality (Sprague, 1946). BSCB1 was developed in the 1940s from 12 inbred lines chosen for resistance to whorl-leaf feeding by the European corn borer (*Ostrinia nubilalis* Hübner) (Hallauer et al., 1974).

Procedures used in the first five cycles were described by Penny and Eberhart (1971). Several significant changes were made in the program after Cycle 1 (C1) of selection. Random mating of the newly synthesized populations was dropped in C2 to reduce the number of generations per cycle and to allow pedigree records to reduce the rate of inbreeding. Beginning with C6, S_1 lines were used to create the half-sib families for evaluation. The use of S_1 lines allowed selection among and within lines for greater genetic advance per cycle. Evaluation trials after C5 of selection were machine-harvested without gleaning; all previous evaluation trials had been hand-harvested. After C8, 20 parents were chosen per population for intermating, as opposed to 10 parents used in previous cycles. The number of parents intermated was increased, to reduce

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Abbreviations: BSSS, Iowa Stiff Stalk Synthetic; BSCB1, Iowa Corn Borer Synthetic no. 1; C*n*, *n*th cycle of selection; RFS, reciprocal full-sib selection; RRS, reciprocal recurrent selection; **, significant at the 0.01 probability level.

random genetic drift. After C9, the program was converted to selection based on full-sib progenies (Keeratinijakal and Lamkey, 1993). Thus, the program is essentially undergoing reciprocal full-sib selection (RFS). There were two reasons for changing the program to RFS: first, the number of plots evaluated could be decreased by half while maintaining selection intensity, or the number of progeny evaluated could be increased and the selection intensity correspondingly increased; second, the genetic gain per cycle is theoretically greater for RFS than for RRS. The primary trait selected has been grain yield, with selection for less grain moisture at harvest and resistance to root and stalk lodging. Beginning with C9, superior progenies were selected by using a selection index weighted by the heritabilities of grain yield, grain moisture, root lodging, and stalk lodging (Smith et al., 1981a,b).

Progenies evaluated in our experiment were developed in the 1988 breeding nursery at the Agronomy and Agricultural Engineering Research Center near Ames, IA. Random S_0 plants from C0, C5, and C11 of BSSS(R) and BSCB1(R) were grown and reciprocal full-sib families were developed for BSSS(R)C0 × BSCB1(R)C0, BSSS(R)C5 × BSCB1(R)C5, and BSSS(R)C11 × BSCB1(R)C11 populations by crossing random pairs of S_0 plants in a biparental-progenies mating design (Hallauer and Miranda, 1988). Reciprocal crosses between plants were made, and ears were bulked to produce enough seed for evaluation.

Families were evaluated at Ames, Ankeny, and Crawfordsville, IA, in 1989 and 1990. The Crawfordsville location was not harvested in 1989 because of severe wind damage late in the season. The experimental sample consisted of 100 reciprocal full-sib families from each of the three interpopulation crosses, for a total of 300 entries. The 300 entries were evaluated in 10 sets of a replications-in-sets design (Comstock and Robinson, 1952). Each set was a randomized complete-block design with two replications. The 30 entries in each set consisted of 10 random reciprocal full-sib families from each of the three interpopulation crosses.

Plots were one row 5.49 m long, with 0.76 m between plots. Plots were overplanted and thinned to a uniform stand density of 52 600 plants ha^{-1} in 1989 and 62 190 plants ha^{-1} in 1990. Plots were machine-planted and harvested with no gleaning of dropped ears. Data were obtained for machine-harvestable grain yield (Mg ha^{-1}) adjusted to 155 g kg^{-1} grain moisture, grain moisture (g kg^{-1}) at harvest, root lodging (% plants leaning greater than 30° from vertical), stalk lodging (% broken at or below highest ear node), plant and ear height (cm), anthesis date (number of days from planting to 50% of plot shedding pollen), and silking date (number of days from planting to 50% of plot with emerged silks). Plant and ear heights were calculated as the average of measurements on 10 competitive plants per plot and were measured after anthesis as distance from soil level to the highest ear-bearing node (ear height) and from soil level to the flag leaf node (plant height). Grain yield, grain moisture, root and stalk lodging, and dropped ears were evaluated at all environments except Crawfordsville in 1989. Plant and ear heights were evaluated at Ames and Ankeny in 1989 and at Ankeny and Crawfordsville in 1990. Anthesis and silking dates were recorded at Ames in 1989 and 1990.

Distribution histograms were constructed by using the means of the 100 full-sib progenies for each population. Distributions were tested for normality by using the Shapiro–Wilk W test statistic (Shapiro and Wilk, 1965). Estimates of skewness and kurtosis were also calculated for each distribution. The coefficient of skewness was estimated as

$$g_1 = \frac{m_3}{(m_2\sqrt{m_2})}$$

where

$$m_3 = \sum_i^n \left[X_i - \sum_i^n X_i/n\right]^3/n$$

and

$$m_2 = \sum_i^n \left[X_i - \sum_i^n X_i/n\right]^2/n$$

The coefficient of kurtosis was estimated as

$$g_2 = \frac{m_4}{(m_2)^2} - 3$$

where

$$m_4 = \sum_i^n \left[X_i - \sum_i^n X_i/n\right]^4/n$$

When the sample population is normally distributed, the coefficients of skewness and kurtosis are approximately normally distributed about zero, with standard deviations of $(6/n)^{1/2}$ for skewness and $(24/n)^{1/2}$ for kurtosis (Snedecor and Cochran, 1989, p. 78–81). Positive coefficients of skewness indicate an elongated upper tail in the frequency distribution, whereas negative coefficients indicate an elongated lower tail. Positive coefficients of kurtosis indicate a distribution with longer tails than expected under normality; negative coefficients indicate a flat-topped distribution.

The analysis of variance was calculated by assuming a random-effects model. Individual analyses of variance for a replications-in-sets design were calculated and combined over environments to obtain the combined analysis of variance. Entry within sets, genotype × environment interaction within sets, and error sources of variation were partitioned into sources for among families within the three interpopulation crosses. Entry-within-sets sources were tested for significance by using the appropriate genotype × environment interaction mean squares. Genotype × environment interaction within sets sources were tested for significance by using the appropriate error mean squares.

Means were calculated for the three interpopulation crosses based on 100 reciprocal full-sib families. Linear regression coefficients were calculated by using weighted least squares to obtain estimates of average rate of response per cycle. The weights were the reciprocals of the variances of cycles means. The variances of cycle means were calculated as the variation among families within sets mean square for the appropriate cycle divided by the number of observations in the mean. Percentage of response per cycle was calculated by dividing the linear regression coefficient by the intercept and multiplying by 100.

Estimates of variance and covariance components were calculated by equating observed mean squares and cross products with expected mean squares and cross products. Approximate 90% confidence intervals for genetic and genotype × environment interaction variance component estimates were calculated using the method of Knapp et al. (1987). Heritability was estimated as the ratio of the genetic variance to the phenotypic variance on a progeny-mean basis. The genetic component of variance therefore is confounded with additive, dominance, and epistatic components and for reciprocal full-sib families is an estimate of half the additive variance and one-fourth of the dominance variance in the interpopulation cross. Estimates of heritability should then be considered as

Table 1. Trait means and linear response per cycle for BSSS(R)C0 × BSCB1(R)C0, BSSS(R)C5 × BSCB1(R)C5, and BSSS(R)C11 × BSCB1(R)C11 maize populations based on 100 full-sib progenies.

Trait†	BSSS(R) × BSCB1(R) C0 × C0	C5 × C5	C11 × C11	Response per cycle
Grain yield, Mg ha^{-1}	3.87	5.01	6.64	0.25**
Grain moisture, g kg^{-1}	189	189	198	0.85**
Root lodging, %	6.6	7.4	4.5	−0.23**
Stalk lodging, %	41.3	39.6	25.1	−1.64**
Plant height, cm	231	236	238	0.59**
Ear height, cm	115	117	114	−0.13
Days to midanthesis	89.0	89.6	89.1	0.01
Days to midsilk emergence	92.2	91.7	90.1	−0.21**

** Significant at the 0.01 probability level.
† Grain yield, grain moisture, and root and stalk lodging were evaluated at five environments, plant and ear heights were evaluated at four environments, and anthesis and silking dates were evaluated at two environments.

an upper limit of the narrow-sense heritability (Lamkey and Hallauer, 1987). Exact 90% confidence intervals for heritability were calculated by using the method of Knapp et al. (1985). Differences between cycles for estimates of variance components and heritability were declared significant when the confidence intervals for the two cycles did not overlap. Genotypic and phenotypic correlations among traits were estimated as the genotypic or phenotypic covariance divided by the square root of the product of the genotypic or phenotypic variances, respectively.

Estimated inbreeding levels of the populations per se were calculated using the formula presented by Sprague and Eberhart (1977). The effective population size was assumed to be $2N$, where N equals the number of progeny intermated. The number of progeny intermated per cycle was taken from Lamkey et al. (1991). This method should be considered an underestimate because parents probably do not contribute equally to the next generation, and this method does not account for the effects of selection.

RESULTS

Mean grain yield across all environments was 5.17 Mg ha^{-1}. The highest average environmental yield was 6.48 Mg ha^{-1} (Ames, 1989); the lowest was 3.42 Mg ha^{-1} (Ankeny, 1989), due to drought conditions. Winds late in the season at three environments (Ames and Ankeny, 1989; Ames, 1990) gave good stalk lodging differentiation. Few plants were root lodged or had dropped ears in most of the environments.

Response to selection for all traits except grain moisture was in the desired direction. Linear regression coefficients were significant for all traits, except ear height and anthesis date (Table 1). Mean grain yield increased from 3.87 Mg ha^{-1} for BSSS(R)C0 × BSCB1(R)C0 to 6.64 Mg ha^{-1} for BSSS(R)C11 × BSCB1(R)C11, representing a total gain of 71.6%. Grain yield increased at an average rate of 0.25** Mg ha^{-1}, or 6.46% per cycle. Mean stalk lodging decreased 39.2%, relative to C0, after 11 cycles of selection. The C11 plants were 7 cm taller, with ears 1 cm lower than C0 plants. The anthesis–silking delay decreased from 3.2 d in C0 to 1.0 d in C11. Grain moisture remained relatively stable, increasing only 9 g kg^{-1} between the C0 and C11 hybrids.

The distribution of grain yield remained normal after 11 cycles of selection, but did acquire a significant left skew and significantly longer tails than expected under normality (Table 2). Standard errors of skewness and kurtosis coefficients were 0.24 and 0.49, respectively. Shapiro–Wilk values generally remained stable over cycles, although values did decline for stalk lodging, dropped ears, and anthesis and silking dates. Grain moisture, plant height, and ear height frequency distributions had larger Shapiro–Wilk values for the later cycles of selection, indicating that they have a more nearly normal distribution than the C0 × C0 population. Mean grain yield increased nearly six standard deviations, while the range of the distribution decreased one standard deviation (Fig. 1).

Estimates of genetic variance for grain yield for all three cycles were significantly different from zero (Table 3). The estimate of the genotype × environment interaction variance for grain yield of the C11 × C11 population was not significantly different from zero. Estimates of genetic variance for all other traits were significantly different from zero, except for root lodging in the C11 × C11 population. Estimates of genotype × environment interaction variance were relatively small for plant and ear heights and anthesis and silking dates.

Genetic variance of grain yield decreased after 11 cycles of selection, although approximate confidence intervals indicate that genetic variances for C0 × C0 and C11 × C11 populations were not significantly different (Table 3). Genotype × environment interaction variance for grain yield decreased after selection to a level not significantly different from zero. Root lodging, stalk lodg-

Table 2. Shapiro–Wilk (W) test of normality and estimates of coefficients of skewness and kurtosis for frequency distributions of BSSS(R) × BSCB1(R) maize populations.

Trait§	Population	W¶	Coefficient of skewness	Coefficient of kurtosis
Grain yield, Mg ha^{-1}	C0 × C0	0.97	0.10	0.87†
	C5 × C5	0.98	0.05	−0.43
	C11 × C11	0.97	−0.56†	1.02†
Grain moisture, g kg^{-1}	C0 × C0	0.96*	0.16	−0.66†
	C5 × C5	0.98	0.48†	0.76
	C11 × C11	0.98	0.32	0.10
Root lodging, %	C0 × C0	0.90**	1.01‡	0.51
	C5 × C5	0.90**	1.30‡	2.09‡
	C11 × C11	0.91**	1.04‡	0.76
Stalk lodging, %	C0 × C0	0.98	0.14	0.29
	C5 × C5	0.98	0.30	−0.05
	C11 × C11	0.96*	0.41†	−0.25
Plant height, cm	C0 × C0	0.98	−0.30	−0.13
	C5 × C5	0.97	0.12	−0.61
	C11 × C11	0.99	0.16	0.92†
Ear height, cm	C0 × C0	0.96*	−0.36	−0.55
	C5 × C5	0.98	0.12	−0.18
	C11 × C11	0.98	0.11	−0.39
Days to midanthesis	C0 × C0	0.99	−0.19	0.40
	C5 × C5	0.97	0.42†	1.50‡
	C11 × C11	0.97	−0.06	−0.06
Days to midsilk emergence	C0 × C0	0.97	−0.35	−0.05
	C5 × C5	0.96*	0.55†	0.98†
	C11 × C11	0.96*	0.56†	0.92†

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
†,‡ Significant at approximately the 0.10 and 0.02 probability levels, respectively.
§ Grain yield, grain moisture, and root and stalk lodging were evaluated at five environments, plant and ear heights were evaluated at four environments, and anthesis and silking dates were evaluated at two environments.
¶ Shapiro and Wilk (1965) W-test statistic for normality.

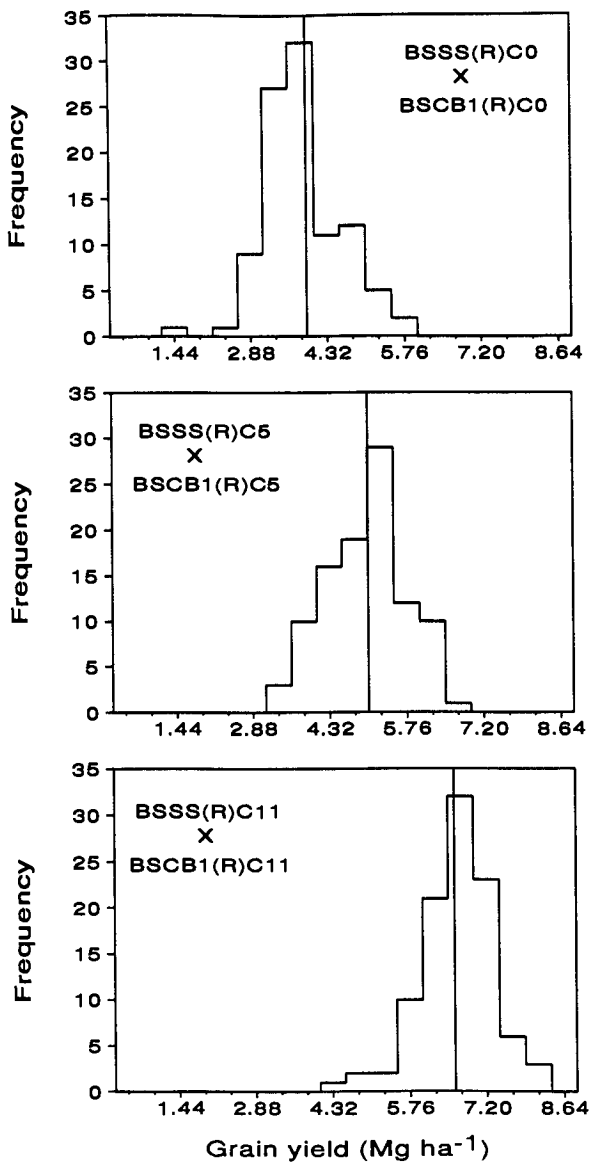

Fig. 1. Frequency distribution for grain yield of 100 full-sib progenies from BSSS(R)C0 × BSCB1(R)C0, BSSS(R)C5 × BSCB1(R)C5, and BSSS(R)C11 × BSCB1(R)C11 maize populations. Distances between class intervals are phenotypic standard deviations of the BSSS(R)C0 × BSCB1(R)C0 population. Vertical lines represent the means of the populations.

ing, anthesis date, and silking date had significant decreases in genetic variance after 11 cycles of selection. Genotype × environment interaction variance decreased significantly for stalk lodging and silking date. Similar to genetic variance, decrease in heritability for grain yield was not significant. Heritability decreased significantly for root and stalk lodging; heritabilities for height and flowering date traits remained high across cycles of selection.

Grain yield had significant phenotypic correlations with grain moisture, stalk lodging, plant height, and ear height in all three population crosses (Table 4). Grain yield was also significantly correlated with anthesis and silking dates in the C5 × C5 population. Other significant correlations generally occurred among height and flowering date traits. Phenotypic correlations showed no consistent pattern or trend over cycles of selection. Genotypic correlations had trends similar to the phenotypic correlations with grain yield having greatest correlations with grain moisture, stalk lodging, plant height, and ear height (Table 4). Genotypic correlations increased among height and flowering date traits after selection, but trends in correlations among other traits were not as obvious.

DISCUSSION

Reciprocal recurrent selection has been effective for improving mean grain yield in the BSSS × BSCB1 population cross. The estimated rate of gain in our study, 0.25 Mg ha^{-1} (6.46%) per cycle, agreed well with the estimates obtained by Keeratinijakal and Lamkey (1993) of 0.28 Mg ha^{-1} (6.95%) per cycle, by Smith (1983) of 0.247 Mg ha^{-1} per cycle for C0 to C4 and 0.361 Mg ha^{-1} per cycle for C4 to C8, and by Eberhart et al. (1973) of 0.273 Mg ha^{-1} per cycle. Studies conducted earlier than these generally had lower rates of gain, which may have been due to their use of hand harvesting and gleaning as pointed out by Smith (1983).

Genetic variance for grain yield decreased with cycles of selection, although the genetic variance of the C11 × C11 population was not significantly different from that of the original population cross. Frequency distributions for grain yield also indicate that the population cross was improved without loss of normality (Fig. 1). Improvement of mean grain yield in BSSS(R) × BSCB1(R) seems to have had little effect on the features of the frequency distribution, which agrees with the results of Moll et al. (1977). These factors indicate that RRS has increased the mean of the population cross without significant loss of genetic variation for improvement in future cycles of selection. Hallauer (1984) examined genetic variance among full-sib progenies between BS10 and BS11 and similarly found no significant decrease after seven cycles of RFS.

Hallauer (1970) estimated variance components in the C0 × C0 and C4 × C4 interpopulation crosses of BSSS and BSCB1. He reported that additive variance decreased significantly in the interpopulation cross and that dominance variance decreased from C0 to C4, but the difference was not significant. Calculating the genetic variance among full-sib families for grain yield (Mg ha^{-1}) as half the additive variance plus one-fourth the dominance variance gives a reduction from 0.22 in C0 × C0 to 0.10 in C4 × C4. The reasons for the difference between our results and Hallauer's results are not evident. The results from the two studies may not be directly comparable, because in Hallauer's study the interpopulation crosses were random-mated three generations before estimating variance components, plots were hand-harvested, and grain yield was reported on a per-plant basis.

Eleven cycles of RRS have improved other agronomic traits in addition to grain yield. Mean stalk lodging has decreased 1.64% per cycle after 11 cycles of selection. Greater response was observed between C5 and C11, indicating that indirect selection due to machine harvesting has been effective in reducing stalk lodging. Results obtained by Keeratinijakal and Lamkey (1993) are

Table 3. Estimates of variance components and heritabilities with confidence intervals for BSSS(R) × BSCB1(R) maize populations.

Trait†	Population	Genetic variance	Confidence limits‡ Lower bound	Confidence limits‡ Upper bound	Genotype × environment variance	Confidence limits‡ Lower bound	Confidence limits‡ Upper bound	h^2	Confidence limits§ Lower bound	Confidence limits§ Upper bound
Grain yield, Mg ha^{-1}	C0 × C0	0.34	0.23	0.50	0.23	0.10	0.38	64.7	52.9	72.9
	C5 × C5	0.32	0.20	0.49	0.32	0.17	0.49	59.3	45.7	68.7
	C11 × C11	0.23	0.14	0.35	0.03	−0.11	0.17	56.6	42.1	66.6
Grain moisture, g kg^{-1}	C0 × C0	73.0	50.9	103.9	62.4	42.7	84.3	71.0	61.3	77.7
	C5 × C5	97.9	71.3	134.8	31.8	12.8	51.2	79.1	72.1	83.9
	C11 × C11	60.0	40.3	87.6	61.2	40.0	84.0	65.7	54.2	73.6
Root lodging, %	C0 × C0	11.95	6.98	18.81	16.02	8.51	24.06	52.8	37.0	63.7
	C5 × C5	9.18	4.23	15.97	21.19	12.13	30.94	41.3	21.7	54.9
	C11 × C11	1.25	−1.06	4.32	11.25	5.13	17.75	12.8	−16.4	32.9
Stalk lodging, %	C0 × C0	67.77	48.47	94.75	45.35	30.56	61.62	75.3	67.1	81.0
	C5 × C5	60.57	44.00	83.76	9.35	−3.80	22.76	78.2	71.0	83.3
	C11 × C11	16.86	10.31	25.94	14.18	4.51	24.32	56.2	41.5	66.3
Plant height, cm	C0 × C0	130.5	100.5	172.6	1.3	−6.3	9.3	92.5	89.9	94.3
	C5 × C5	75.4	57.2	100.8	3.4	−3.3	10.7	88.6	84.7	91.3
	C11 × C11	78.3	60.2	103.7	−3.4	−8.6	1.9	92.2	89.5	94.1
Ear height, cm	C0 × C0	102.6	78.9	135.8	7.7	2.1	14.0	92.2	89.5	94.0
	C5 × C5	59.9	45.4	80.1	6.5	1.4	12.2	88.4	84.4	91.2
	C11 × C11	82.0	63.1	108.5	1.5	−3.2	6.6	92.5	89.9	94.3
Days to midanthesis	C0 × C0	3.15	2.37	4.23	0.29	0.07	0.58	87.4	82.1	91.1
	C5 × C5	1.77	1.30	2.41	−0.01	−0.23	0.25	82.2	74.8	87.4
	C11 × C11	1.25	0.88	1.74	0.14	0.07	0.40	75.7	65.6	82.9
Days to midsilk	C0 × C0	4.62	3.33	6.38	1.25	0.68	2.02	78.9	70.1	85.1
	C5 × C5	2.40	1.76	3.28	0.08	−0.21	0.42	82.3	74.9	87.5
	C11 × C11	2.07	1.52	2.83	0.10	−0.15	0.40	82.1	74.6	87.3

† Grain yield, grain moisture, and root and stalk lodging were evaluated at live environments, plant and ear heights were evaluated at four environments, and anthesis and silking dates were evaluated at two environments.
‡ Approximate 90% confidence interval.
§ Exact 90% confidence interval.

comparable to this study, with a reduction in stalk lodging of 1.52% per cycle. Mean root lodging also decreased with cycles of selection. The switch to machine harvesting of yield trials seems to have also aided selec-

Table 4. Phenotypic (above diagonal) and genotypic (below diagonal) correlations among traits based on 100 full-sib progeny means from BSSS(R) × BSCB1(R) maize populations.

Trait†	Population	Grain yield	Grain moisture	Root lodging	Stalk lodging	Plant height	Ear height	Days to Mid-anthesis	Days to Midsilk emergence
Grain yield, Mg ha^{-1}	C0 × C0		0.31**	−0.02	−0.38**	0.51**	0.34**	0.06	−0.14
	C5 × C5		0.38**	−0.08	−0.64**	0.39**	0.29**	0.31**	0.24*
	C11 × C11		0.33**	0.19	−0.28**	0.39**	0.30**	0.14	0.12
Grain moisture, g kg^{-1}	C0 × C0	0.50		0.18	−0.06	0.47**	0.37**	0.39**	0.33**
	C5 × C5	0.58		0.07	−0.31**	0.22*	0.29**	0.51**	0.49**
	C11 × C11	0.61		0.21*	−0.14	0.34**	0.30**	0.34**	0.45**
Root lodging, %	C0 × C0	−0.01	0.32		−0.02	0.25*	0.17	0.17	0.19
	C5 × C5	−0.22	0.07		0.14	0.14	0.03	0.11	0.09
	C11 × C11	0.72	0.79		0.01	0.15	0.22*	0.10	0.07
Stalk lodging, %	C0 × C0	−0.45	−0.07	−0.02		−0.00	0.18	−0.03	−0.35**
	C5 × C5	−0.80	−0.40	0.26		−0.19	−0.07	−0.32**	−0.32**
	C11 × C11	−0.30	−0.20	0.03		0.16	0.27**	−0.06	−0.15
Plant height, cm	C0 × C0	0.68	0.59	0.37	−0.02		0.79**	0.51**	0.12
	C5 × C5	0.51	0.27	−0.25	0.25		0.81**	0.55**	0.44**
	C11 × C11	0.60	0.46	0.34	0.21		0.86**	0.64**	0.57**
Ear height, cm	C0 × C0	0.47	0.47	0.27	0.18	0.80		0.58**	0.04
	C5 × C5	0.40	0.36	−0.11	0.06	0.83		0.54**	0.43**
	C11 × C11	0.48	0.41	0.57	0.34	0.89		0.72**	0.60**
Days to midanthesis	C0 × C0	0.16	0.50	0.33	−0.02	0.60	0.64		0.74**
	C5 × C5	—‡	0.69	0.35	−0.49	0.69	0.67		0.86**
	C11 × C11	0.30	0.38	0.14	−0.14	0.79	0.84		0.90**
Days to midsilk emergence	C0 × C0	−0.08	0.41	0.41	−0.26	0.17	0.06	0.82	
	C5 × C5	—	0.71	0.13	−0.43	0.57	0.51	0.95	
	C11 × C11	0.35	0.59	0.15	−0.30	0.72	0.68	0.94	

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Grain yield, grain moisture, and root and stalk lodging were evaluated at five environments, plant and ear heights were evaluated at four environments, and anthesis and silking dates were evaluated at two environments.
‡ Genotypic correlation not calculated because of negative estimate of genetic variance.

tion for reduced root lodging, because the reduction occurred between C5 and C11.

Genetic variance estimates for root and stalk lodging decreased significantly, as expected. Selection for improvement in these traits has increased the frequency of favorable alleles. Genetic variance and heritability estimates for root lodging have decreased to a level not significantly different from zero, which indicates that little improvement via selection can be made for this trait in the population cross.

Mean plant height increased 7 cm in our study, whereas Keeratinijakal and Lamkey (1992) reported a 14-cm increase. Mean ear height decreased 1 cm, but a 2-cm increase was reported by Keeratinijakal and Lamkey (1993). Genetic variance estimates for plant and ear height decreased nonsignificantly from C0 to C5. The reduction may have been due to early selection for uniform plant height. Phenotypic and genotypic variances decreased at similar rates, as indicated by the relatively stable estimates of heritability across cycles.

Estimates of mean anthesis and silking dates indicate that silks are emerging earlier and that anthesis date has remained relatively stable across cycles. The average rate of gain per cycle of -0.21 d for silking date estimated from our study is similar to the -0.24 estimate obtained by Keeratinijakal and Lamkey (1993). Significant or nearly significant reductions in genetic variance occurred among each of the three cycles tested for anthesis and silking date, whereas heritability estimates remained relatively stable.

Estimates of phenotypic and genotypic correlations among traits did not seem to be affected by selection for yield. Highly correlated traits in the C0 × C0 population were generally highly correlated in the C5 × C5 and C11 × C11 populations; traits having low correlations in the C0 × C0 population generally maintained that low correlation after 11 cycles of selection. The stability of correlations across cycles of selection was consistent with results obtained by Walters et al. (1991).

Estimated inbreeding levels were zero for BSSS and BSCB1, 0.23 for BSSS(R)C5 and BSCB1(R)C5, and 0.37 for BSSS(R)C11 and BSCB1(R)C11. The greatest proportion of inbreeding occurred during the first eight cycles of selection, when only 10 parental lines were selected for intermating within each population per se. This differs from the trend of genetic variance, which shows the greatest decrease between C5 and C11. Although random genetic drift and small effective population sizes can decrease genetic variance, the estimated inbreeding level of the populations per se does not seem to correspond to the rate of loss of genetic variance in the population cross.

The results obtained in our study corroborate the results of Keeratinijakal and Lamkey (1993). Reciprocal recurrent selection has been effective for improving the mean performance of the population cross for grain yield, root lodging, and stalk lodging, with small or desirable changes in other agronomic traits. There was no evidence for a reduction in genetic variance for grain yield, although significant reductions were found for root and stalk lodging and anthesis and silking dates. These results suggest that future selection response should be maintained at or near current rates of progress.

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